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TERRITORY SELECTION BY UPLAND RED-WINGED BLACKBIRDS IN EXPERIMENTAL RESTORATION PLOTS

MARIA A. FUREY[1,3] AND DIRK E. BURHANS[2,4]

ABSTRACT.—We examined territory selection of Red-winged Blackbirds (*Agelaius phoeniceus*) in experimental treatments with varied groundcovers and densities of planted and naturally occurring oaks (*Quercus* spp.) used by blackbirds for perching. We also compared vegetation parameters between blackbird territories and unused (i.e., unoccupied by Red-winged Blackbirds) areas. Although perch densities were greater in blackbird territories in unplanted controls and oak-planted treatments without redtop grass (*Agrostis gigantea*) than they were in unused areas, the low densities of perches in territories planted with redtop grass indicate that perch density is not limiting above some lower threshold. Territories, particularly in treatments with no redtop, tended to have greater mean grass cover and taller grass heights than unused areas. Our results are consistent with other studies in finding that Red-winged Blackbirds prefer areas having tall vegetation and dense grass. *Received 14 July 2005, accepted 21 February 2006.*

A large body of observational studies has documented relationships between avian abundance, or territory use, and vegetation parameters. Examples include studies comparing differences among songbird territories with respect to vegetation height or litter depth (Wiens 1969) and grass or shrub cover (Rotenberry and Wiens 1980), and those that relate avian abundance to vegetation density (Orians and Wittenberger 1991) or grass (Scott et al. 2002). However, important relationships between vegetation and habitat use can be obscured if the variation among study sites (or plots) is minimal (Orians and Wittenberger 1991, Pribil and Picman 1997). One way to elucidate habitat variation and distinguish factors important in habitat selection is by comparing sites that differ explicitly in terms of vegetation management. For example, Shochat et al. (2005), Wood et al. (2004), and Murkin et al. (1997) evaluated avian responses among plots that varied with respect to management regime, and were able to make clear inferences that may have been obscured had they studied only unmanaged habitats.

Even where variation among plots is made explicit, however, the influences of vegetative factors on avian settlement patterns may be masked if measurements are made at inappropriate scales (Orians and Wittenberger 1991, Pribil and Picman 1997). For example, Orians and Wittenberger (1991) found that Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) settle according to food supplies at the scale of an entire marsh, a relationship that was not apparent at the territory scale. Similarly, Burhans (1997) found that some factors explaining brood parasitism at the nest-site scale were relevant only when considered at the larger scale of habitat.

We investigated the role of vegetation structure in the selection of breeding territories by Red-winged Blackbirds (*Agelaius phoeniceus*) in two experimentally manipulated restoration sites of floodplain oak (*Quercus* spp.) near the Missouri River. Numerous researchers have investigated habitat selection by Red-winged Blackbirds (Albers 1978, Joyner 1978, Pribill and Picman 1997, Turner and McCarthy 1998), and some have examined responses of Red-winged Blackbirds and other species within plots characterized by differing management regimes (Herkert 1994, McCoy et al. 2001, LaPointe et al. 2003); however, our study is the only one we know of in which more than one factor varied (i.e., perch availability and grass cover) among adjoining treatment plots within the same sites. These plots varied with respect to densities of planted trees, which blackbirds used as perches, and the presence or absence of a planted cover crop. Typically, managed plots in other songbird studies have been geographically sepa-

[1] Dept. of Forestry, 203 Natural Resources Bldg., Univ. of Missouri, Columbia, MO 65211-7270, USA.
[2] Dept. of Fisheries and Wildlife Sciences, Natural Resources Bldg., Univ. of Missouri, Columbia, MO 65211-7270, USA.
[3] Current address: P.O. Box 7021, Columbia, MO 65205-7021, USA.
[4] Corresponding author; e-mail: burhansd@missouri.edu

rated (Herkert 1994, Swengel 1996, McCoy et al. 2001); however, our plots shared common boundaries to allow comparisons of habitat selection without the confounding effects of between-site variation.

We specifically wished to determine (1) how the availability of perches and vegetation determines Red-winged Blackbird territory use and density at the treatment scale, and (2) how within-treatment vegetation composition and structure in territories would compare with unused (i.e., unoccupied by Red-winged Blackbirds) areas. We were particularly interested in determining the importance of grass cover and density, because a dense, short-stature cover crop of grass (redtop, *Agrostis gigantea*) planted at our sites had suppressed invading vegetation but was unsuitable for nesting, whereas the common invasive—Johnsongrass (*Sorghum halepense*), which was also present—potentially provided a tall nesting substrate and cover. Because blackbirds in upland settings prefer dense, tall cover (Albers 1978, Bollinger 1995), we predicted that density of blackbird territories would be greater in treatments not planted with redtop. Within treatments, we predicted that blackbird territories would be characterized by denser, taller cover than unused areas. Based on previous studies establishing the importance of perches (Joyner 1978, Payne et al. 1998), we predicted that densities of Red-winged Blackbird territories would be greater in treatments planted with oaks, and that territories would have perches located at greater heights and at greater densities than unused areas.

METHODS

Study site.—Our research was conducted in central Missouri at two sites located within the Missouri River Floodplain. Plowboy Bend Conservation Area (38° 48′ 5″ N, 92° 24′ 17″ W), a landscape dominated by row-crop agriculture, is located west of the Missouri River's main channel within a levee-protected floodplain. Smoky Waters Conservation Area (38° 35′ 9″ N, 91° 58′ 3″ W) is located 72 km southeast of Plowboy Bend, between the Missouri River's main channel and the Osage River. Smoky Waters' floodplain has not been protected since a levee was breached there in the 1993 and 1995 floods; thus, it is subject to occasional flooding.

Both study sites encompassed three 16.2-ha, adjacent experimental treatments (hereafter, "blocks") that differed with respect to vegetation treatments. The blocks—formerly row-cropped—were established in 1999 for an ongoing research project to evaluate the restoration of hard mast (oak acorn; Dey et al. 2003). Oaks were planted at a density of 119 trees/ha (Dey et al. 2003). During our study, half of the planted oaks were >1.5 m high and were often used as perches by Red-winged Blackbirds (MAF pers. obs.). Each site had three treatment blocks with varying densities of planted and natural perches. (1) "Redtop" blocks, seeded with a uniform cover of redtop grass, were planted with saplings of swamp white (*Quercus bicolor*) and pin (*Q. palustris*) oaks distributed in planting units that varied in terms of planting methods but had a uniform ground cover of redtop grass (for details, see Dey et al. 2003). The redtop grass produced a low, dense ground cover that largely suppressed invasion by other herbaceous and woody vegetation that otherwise may have been used as perches or nest sites by Red-winged Blackbirds; thus, redtop blocks contained some planted oak perches but few or no natural perches. (2) "No redtop" blocks contained the same configuration of oak plantings described above for redtop blocks, but they were not seeded with a ground cover; therefore, over time they contained taller, denser shrubs, trees, and herbaceous vegetation and more "natural" unplanted perches than redtop blocks. (3) "Control" blocks contained only natural perches, such as invading forbs and shrubs, and no oak plantings or any of the vegetation treatments listed above.

Delineation of breeding territories.—We identified breeding territories from March to May in 2001 and 2002 by monitoring male Red-winged Blackbirds exhibiting mating behaviors, such as the "song spread" (Yasukawa and Searcy 1995) and territory defense. To delineate territories, we conducted consecutive flushing (Wiens 1969), a technique in which males are approached and followed until they alight on the perches that define their territory. Territories were delineated by identifying and flagging at least four perches used consecutively by each male (mean number of perches flagged/territory = 7.12 ± 1.97 SD).

Vegetation measurements.—Once a breeding territory was completely flagged, we recorded the location, species, and height (m) for each perch. We established two 1-m-wide belt transects in each territory to estimate density of potential perches (no. stems >1.5 m tall/m^2) and determined average maximum stem height (m). To establish the first transect, the center of the territory was visually located and staked; then a random azimuth was determined to establish the direction of the transect across the territory. The second transect location was established perpendicular to the first. Using a 1-m stick held horizontally at 1.5 m above ground, we walked the territory end-to-end along each transect, recording the number of stem contacts and the maximum vegetation height (m) at 1-m intervals. Two vertical density-board measurements were taken at random locations along each transect, resulting in four individual measurements of vertical vegetation structure for each breeding territory. The proportion of vertical vegetation was estimated using a 9-increment density board (2.25 m tall × 0.25 m wide). At each 0.25-m increment, we estimated the proportion of living and dead vegetation from a distance of 15 m. We estimated the proportion in each increment for woody, forb (herbaceous), and grass vegetation and combined them to generate an estimate of mean total proportion.

We randomly located unused plots (unoccupied by Red-winged Blackbirds) by using a 100-m interval grid of UTM (Universal Transmercator) coordinates placed over the restoration sites where there were no active territories. Sampling of vegetation structure was identical to that conducted within blackbird territories, with the exception that belt-transect length within a given site was based on the average belt-transect length of all breeding territories found at the site.

Statistical analyses.—For each year, we calculated territory density for each block type (redtop, no redtop, control) by summing the numbers of territories found in each block type and dividing by 16.2 ha. If a territory straddled more than one block type, we placed it in the block type in which the majority of its area occurred.

We averaged vegetation variables for the four samples taken within each blackbird territory. For vertical vegetation measurements, the mean was calculated from all of the 0.25-m increments for each vegetation type of interest (woody, forb, grass, and total vertical vegetation). Of the vertical vegetation measurements, we included only mean total vertical cover, mean vertical grass cover, and mean grass height, which was defined as the last-recorded increment having grass cover on the vertical density board. We reasoned that mean total vertical cover was important if blackbirds were assessing territories based on cover without regard to vegetation type. We examined grass cover and height because of the apparent differences in grass cover between redtop blocks and the other block types.

We also used the vertical vegetation measurements to create a variable called "threshold nest-cover height," defined as the lowest height at which mean total vertical cover (based on the density board samples) was ≥60%. The latter value was based upon a 2001 sample of vegetation measured (using the same vertical density board methodology described above) at 99 Red-winged Blackbird nests. At the 99 nests, we determined that the mean total vertical cover at nest height (viewed 15 m from the board) was 60%; therefore, we assumed that blackbirds select nest sites with at least 60% total vertical cover. Typically, total vertical cover approached 100% near the ground, but decreased with distance above ground; thus, a high value of threshold nest-cover height (i.e., >60%) usually indicated denser cover below the threshold height, but less cover above. High values of threshold nest-cover height do not indicate that vertical cover was denser; rather, they indicate that the vertical height at which cover equaled or exceeded 60% was greater.

We used a general linear model (PROC MIXED; SAS Institute, Inc. 2003) to test for differences in territory density among block types. We nested block within site as a random effect to account for differences in site, and included "year" in the model to account for additional variation. We used the likelihood ratio test to test the overall model against a null model that included only the intercept. If the overall model was significant, we used the LSMEANS statement to examine whether territory densities varied among the three block types (control, no redtop, redtop); we considered differences at $P \leq 0.05$ to be significant.

We analyzed vegetation differences among block types, by site, using PROC MIXED models as above, again using likelihood ratio tests to compare models against a null model. Because there were a large number of vegetation variables, for which one or several tests could be significant by chance, we used the sequential Bonferroni method to interpret overall model significance (Rice 1989). Although the sequential Bonferroni test has been criticized as overly conservative in circumstances where numerous individual tests show moderately significant results (Moran 2003), in this circumstance we feel that it was a suitable compromise between having no control for type I error and the simple Bonferroni test, which is even more conservative (Rice 1989). If the overall model was significant, we used the LSMEANS statement to determine whether territory area and vegetation variables varied among the three block types (control, no redtop, redtop), by site; within each model, we considered differences at adjusted $P \leq 0.05$ to be significant.

We also compared parameters of vegetation structure between areas occupied ("territories") and unoccupied ("unused" plots) by Red-winged Blackbirds to describe local vegetation differences affecting blackbird habitat selection within blocks. Because flooding events in 2001 prevented us from sampling unused plots at both sites, only 2002 field data were used for this analysis, and we removed territory and unused samples entirely if any data values were missing. We used a general linear model (PROC MIXED; SAS Institute, Inc. 2003) with an LSMEANS statement to calculate means and standard errors for each variable of interest. We determined that there were differences among territories and unused plots if likelihood ratio tests indicated overall model significance, based on sequential Bonferroni adjustments for the six vegetation variables analyzed. If the overall model was significant, we evaluated multiple comparisons among different combinations of block, territory, and unused plots (15 comparisons per model) with sequential Bonferroni tests to control for type I error.

RESULTS

We analyzed 81 Red-winged Blackbird breeding territories across both sites and years. Mean breeding territory area in 2001 was 1,667 ± 195 m^2 (n = 19), 1,897 ± 221 m^2 (n = 17), and 2,310 ± 464 m^2 (n = 10) in redtop, no redtop, and control blocks, respectively, and in 2002 it was 1,648 ± 173 m^2 (n = 14), 1,808 ± 269 m^2 (n = 17), and 771 ± 83 m^2 (n = 4). We found no differences in territory area by block type (likelihood ratio test: $\chi^2 = 2.3$, df = 3, $P = 0.51$). In 2001, mean territory density across both sites was 0.71 ± 0.74, 0.67 ± 0.26, and 0.31 ± 0.26 territories/ha in redtop, no redtop, and control blocks, respectively. In 2002, mean territory density across both sites was 0.46 ± 0.66, 0.56 ± 0.17, and 0.12 ± 0.17 territories/ha; there were no blackbird territories in redtop or control blocks at Plowboy Bend during this year. Territory density did not differ among blocks or years (likelihood ratio test: $\chi^2 = 5.8$, df = 3, $P = 0.12$).

We did not find differences among the three block types for mean perch density, mean total vertical cover, or mean vertical grass cover (Fig. 1A, C, E). The model for mean perch height differed significantly from the null model ($\chi^2 = 39.0$, df = 3, adj. $P < 0.001$), but the differences were among years (2001: 2.16 ± 0.03 m; 2002: 1.82 ± 0.04 m; $t = 6.73$, df = 74, $P < 0.001$); there were no differences in perch height among blocks (Fig. 1B). Similarly, models for mean threshold nest-cover height and grass height differed from null models, but again differences were among years rather than blocks (threshold nest-cover height model: overall $\chi^2 = 17.0$, df = 3, adj. $P < 0.01$; mean grass height model: overall $\chi^2 = 28.6$, df = 2, adj. $P < 0.008$; Fig. 1D, F). Mean grass height across all territory blocks was greater in 2001 (2001: 0.53 ± 0.02 m; 2002: 0.36 ± 0.02 m; $t = 5.53$, df = 74, $P < 0.001$), whereas mean threshold nest-cover height was shorter in 2001 (2001: 0.40 ± 0.06 m; 2002: 0.63 ± 0.06 m; $t = -4.30$, df = 74, $P < 0.001$).

We used samples from 35 Red-winged Blackbird breeding territories and 35 unused plots (2002 data only) to compare vegetation in breeding territories with that in unused plots (n = 10, 13, and 12 unused plots sampled from both sites combined in redtop, no redtop, and control blocks, respectively). Models testing for differences between territories and unused plots did not differ from

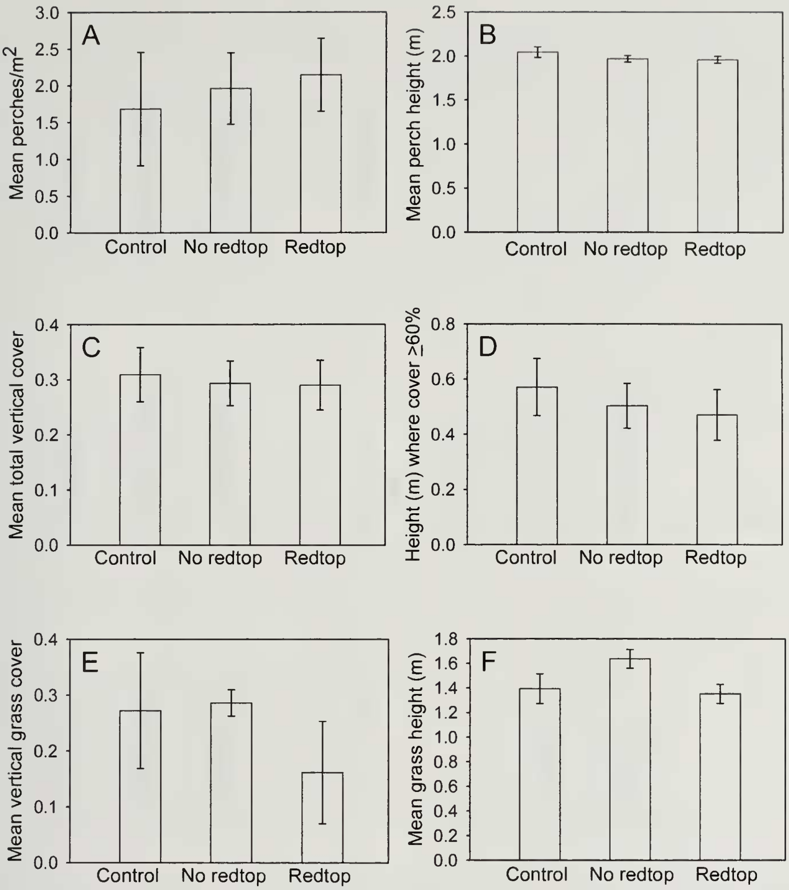

FIG. 1. Vegetation cover (expressed as a proportion), height, and perch density comparisons (±SE) among treatment blocks at Plowboy Bend and Smoky Waters Conservation Areas, Missouri, 2001–2002.

null models with respect to perch height (Fig. 2B), mean total vertical cover (Fig. 2C), or threshold nest-cover height (Fig. 2D). Overall, mean perch density varied among combinations of block and territory or unused plots ($\chi^2 = 28.5$, df = 4, adj. $P < 0.008$; Fig. 2A). Territories in control blocks had greater perch densities than in all other block types, although there were only four control territories in the analysis (all adj. $P \leq 0.005$; Fig. 2A). Perch densities did not differ between other combinations of block and territory or unused plots, except that perch densities were greater in no redtop territories than they were in redtop territories and redtop unused plots (no redtop territories versus redtop territories: $t = 3.42$, df = 61, adj. $P < 0.005$; no redtop territories versus redtop unused plots: $t = 3.01$, df = 61, adj. $P < 0.006$).

Overall, mean vertical grass cover varied among combinations of block and territory or unused plots ($\chi^2 = 21.5$, df = 5, adj. $P < 0.01$). Grass cover was greater in no redtop territories compared with no redtop unused plots, control unused plots, and redtop territories and unused plots (all adj. $P \leq 0.004$; Fig. 2E). Grass height varied overall among combinations of block and territory or unused plots ($\chi^2 = 15.4$, df = 5, adj. $P < 0.01$). Grass height was greater in no redtop territories than in redtop, no redtop, and control unused plots (all adj. $P \leq 0.004$; Fig. 2F).

DISCUSSION

We found no significant differences in territory density or area among treatment blocks, nor did we find differences among vegetation variables by territory treatment block when

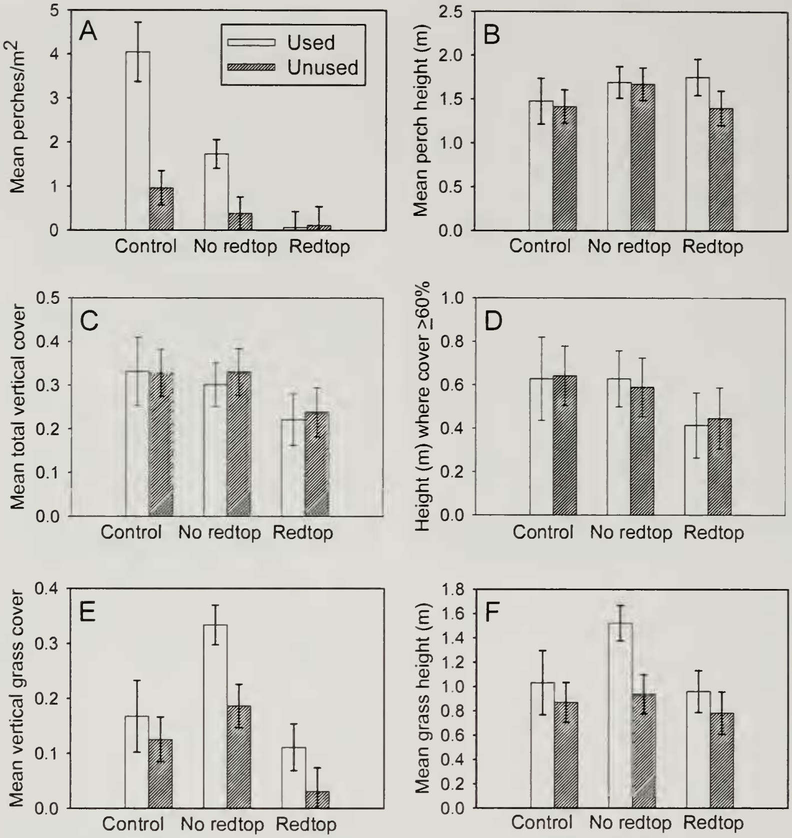

FIG. 2. Vegetation cover (expressed as a proportion), height, and perch density comparisons (±SE) of Red-winged Blackbird territories (used) and unused plots at Plowboy Bend and Smoky Waters Conservation Areas, Missouri, 2002.

2001 and 2002 data were combined. We did find differences, however, between territories and unused plots; generally, blackbird territories were characterized by denser or taller grass cover than unused plots, and territories in control and no redtop blocks tended to contain more perches than unused plots.

In the analysis of territories versus unused plots, the greater perch density in territory blocks with no cover crop (no redtop and control blocks) compared with those that had a cover crop (redtop) may be a reflection of redtop's ability to suppress invasion by trees and shrubs. However, perch density did not differ among territory blocks or years when data from both years were combined (Fig. 1A), whereas the territory/unused analysis, which included only 2002 data, revealed extreme differences in perch density among territory blocks (Fig. 2A). In the case of control territories, perch density could have been an artifact of small sample size, as there were only 4 territories in control blocks in 2002 compared to 10 in 2001. However, upon visual inspection, we detected similar between-year differences in mean perch density in redtop blocks (Fig. 1A versus 2A), and in this case sample sizes were 19 and 14 in redtop territories in 2001 and 2002, respectively. Such inter-annual inconsistencies in bird-vegetation relationships are common and often prevent researchers from reaching direct conclusions in studies of avian-habitat associations (Riffell et al. 2001), including studies of Red-winged Blackbirds (Erckmann et al. 1990) and other blackbirds (Orians and Wittenberger 1991). Red-winged Blackbirds may require only a few perches for territory defense. We noted that blackbirds typically reused the same perches, sometimes frequenting only four or five perches repeatedly (MAF pers. obs.). It may be that perch availability limits blackbird territory settlement only at some lower threshold, in which case even territories with very low perch densities at our sites (e.g., redtop; Fig. 2A) may have met this requirement. Perches have been shown not to limit habitat use by some songbirds (Vickery and Hunter 1995), but at least one study suggests that they are necessary for Red-winged Blackbirds; Joyner (1978) found that even in areas with a preferred grass cover type, blackbirds did not establish territories if fence posts—used as perches—were totally lacking.

In addition to variation in perch density, we also found differences in grass cover and height between territories and unused plots within and among treatment blocks. Variable grass cover, at least within no redtop blocks, suggests that blackbirds may have settled in a non-uniform fashion with regard to grass patches. Although our data did not permit us to relate territories to grass patchiness spatially, overall we did not notice obvious patterns in territory settlement; there were two possible exceptions: (1) the only two blackbird territories in the Plowboy Bend redtop block were very close to blackbird territories on the adjoining no redtop block, from which forbs, shrubs, and Johnsongrass had spread into the redtop block (MAF pers. obs.); and (2) blackbirds tended to avoid settlement along one edge of the Smoky Water control block (MAF pers. obs.). In the second case, we are not sure why blackbirds avoided the block edge, but we believe that settlement in redtop at Plowboy Bend may have been influenced both by the rampant growth of Johnsongrass and by redtop's ability to suppress Johnsongrass and other vegetation. Redtop cover was particularly uniform at Plowboy Bend, where blackbird use of the redtop block was minimal, whereas the redtop block at Smoky Waters underwent extensive invasion of shrubs and forbs (MAF and DEB pers. obs.). Johnsongrass, a dense, stout-stemmed grass that grows to 1.8 m high, was also used as a nesting substrate, whereas redtop was not. Of more than 250 Red-winged Blackbird nests found from 2001–2003, none were anchored in redtop grass, whereas Johnsongrass was among the five most commonly used nest substrates (DEB unpubl. data).

The pattern of denser and taller grass cover in territories, especially in no redtop blocks, generally agrees with other findings in studies of Red-winged Blackbirds. Bollinger (1995) believed that blackbirds occupied his upland sites due to the availability of suitable nest cover and vegetation with stems strong enough to support their nests; results of other studies also indicate that, where stout plants are available, blackbirds choose them as nest sites or for territorial activity (Albers 1978, Joyner 1978, Turner and McCarthy 1998, Kobal et al. 1999). Bollinger (1995) found a positive relationship between presence of grass and blackbirds, and Camp and Best (1994) found a positive relationship between grass cover and nest densities. Other studies have shown that Red-winged Blackbirds favor dense vegetation (LaPointe et al. 2003); Albers (1978) found that blackbird territories had significantly taller, denser vegetation than unused areas, and Bollinger (1995) found that Red-winged Blackbirds were most abundant in fields with dense cover. However, in a survey of Illinois grassland species, Herkert (1994) found no correlates of vegetation structure and occupancy by Red-winged Blackbirds, which were present on 93% of his transects, and Scott et al. (2002) found that blackbirds were negatively associated with grass cover on reclaimed surface mines in Indiana.

Although our 2002 data revealed differences in perch density when comparing territories with unused plots, our results suggest that perch density does not influence Red-winged Blackbird territory selection as long as perch density is above some lower limit. However, particularly in no redtop blocks, blackbirds tended to choose territories that had denser, taller grass cover than that observed in unused plots. This finding is in agreement with other studies, which have shown that Red-winged Blackbirds appear to favor dense vegetation (Albers 1978, Kobal et al. 1999), including tall or dense grass cover (Camp and Best 1994, Bollinger 1995).

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